

Eddie Marsh-Matthews · William J. Matthews

Spatial variation in relative abundance of a widespread, numerically dominant fish species and its effect on fish assemblage structure

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Abstract Collections of fish assemblages from streams in the midwestern United States were used to examine assemblage-level effects of spatial variation in relative abundance of the red shiner, *Cyprinella lutrensis*, a widespread and highly abundant minnow species. This species has been widely introduced outside its native range and is suspected to have impacted local assemblages where it has become established. Given its overall dominance of midwest fish assemblages, and its suspected impact on assemblage structure, we asked if structure of the residual fish assemblages (red shiners excluded) was a function of the relative abundance of red shiners throughout the native range of *C. lutrensis* in the USA. Although red shiner ranked first in abundance in half of the assemblages and numerically dominated 28% of the assemblages, red shiner relative abundance in an assemblage had no detectable effect on richness, diversity, evenness, or complexity of other (residual) species in the assemblage. Relative abundance of red shiners did have a positive effect on the abundance of benthic minnows in the residual assemblage, but not on water column minnows that are ecologically most like red shiners. Environmental factors did not explain a significant amount of the variation in relative abundance of red shiners, but did explain some variation in residual assemblage structure. Although widespread and numerically dominant at many localities, red shiners do not appear to have a strong impact on local fish assemblage structure within their native range. This is in sharp contrast to the reported nega-

tive effects of red shiners on fish assemblages where they have been introduced outside their native range.

Key words Abundance · Community structure · Midwestern USA · Numerically dominant species · Stream fish

Introduction

Numerically dominant species have long been assumed to impact communities at least in proportion to their abundance (an assumption implicit in keystone theory: Power et al. 1996), and there are numerous examples of highly abundant species impacting assemblage structure or ecosystem function, particularly in roles as dominant competitors (Connell 1961; Paine 1974) or ecosystem engineers (Power et al. 1985; Flecker 1996). Recent studies, however, suggest that the impact of a given species on assemblage structure or ecosystem processes may be more a function of species identity, community composition, or membership of that species in a functional group (Symstad et al. 1998). Alternatively, numerically dominant species may have no effect on assemblage properties (e.g., Evans 1989), particularly if the assemblage includes ecologically redundant species (Walker 1992).

Studies addressing the role of a given species in an assemblage or ecosystem typically assay the change in some property of the study system in response to experimental manipulation of abundance of that species (e.g., Paine 1974; Evans 1989; Symstad et al. 1998). Such studies have been valuable in identifying effects of individual species in a system. Among assemblages where a given species tends to dominate numerically, but is variably abundant, studies of assemblage structure over a broad spatial scale can address the more general role of numerically dominant species in communities.

The red shiner, *Cyprinella lutrensis* (Family Cyprinidae), is a widespread and abundant minnow in streams of the Great Plains of the USA (Matthews 1980, 1985).

E. Marsh-Matthews
Oklahoma Biological Survey, University of Oklahoma,
Norman, OK 73019, USA

W.J. Matthews
Sam Noble Oklahoma Museum of Natural History,
Biological Station and Department of Zoology,
University of Oklahoma, Norman, OK 73019, USA

Present address:

E. Marsh-Matthews, Sam Noble Oklahoma Museum
of Natural History and Department of Zoology,
University of Oklahoma, Norman, OK 73019, USA,
emarsh@ou.edu, Fax: +1-405-3257699

Its native range extends from South Dakota to Mexico, and from slightly east of the Mississippi River to the Trans-Pecos in Texas and New Mexico (Matthews 1980). *C. lutrensis* is considered a "widespread generalist" (Matthews 1985): it tolerates extreme temperatures (Matthews and Hill 1979; Matthews and Maness 1979) and low oxygen (Cavin 1971; Matthews 1987), and is an opportunistic insectivore-omnivore (Greger and Deacon 1988; Jennings and Saiki 1990; Cross and Collins 1995). Within its native range, it occurs in a wide variety of habitats (Matthews and Hill 1980; Mayden 1989; Cross and Collins 1995), and is often the most abundant species where it occurs (Matthews 1980).

Red shiners have been introduced extensively outside their native range (Hubbs 1954; Minckley and Deacon 1968; Minckley 1973; Deacon 1988; Jennings and Saiki 1990). They have become numerically dominant in many streams of the American west (Hubbs 1954; Minckley 1991; Ruppert et al. 1993; Gido et al. 1997), where they are suspected to have severely impacted native species or assemblages (Greger and Deacon 1988; Ruppert et al. 1993; Douglas et al. 1994). In Illinois, the range of red shiners has expanded eastward since 1908 (Page and Smith 1970) and expanding populations have hybridized with, and gradually supplanted or displaced native minnows (Burr and Page 1986).

Given its wide distribution, high abundance, and suspected impact on assemblages, *C. lutrensis* is a model organism to investigate assemblage-level effects of spatial variation in abundance of a potentially dominant species. In the present study, we address spatial variation in abundance of *C. lutrensis* over much of the native range, using a large series of standardized, time-delimited collections of fish assemblages throughout the midwest. We investigate patterns of relative abundance of *C. lutrensis*, and its relationship to the structure of the assemblages in which *C. lutrensis* occurs. We examine spatial pattern, environmental factors associated with variation, and the extent to which variation in red shiner numerical dominance explains spatial variation in structure among fish assemblages. In this context, we tested the specific hypothesis that residual assemblages at sites dominated by red shiners would have a fundamentally different structure than residual assemblages where red shiners were present in low numbers.

Materials and methods

Fish assemblages within the range of *C. lutrensis* (Matthews 1980) were sampled at 65 sites in the midwestern United States, from Nebraska and Iowa to south Texas. Red shiners were present at 50 of these sites (Fig. 1), and we restrict our analyses of red shiner abundance to those 50 sites, in order to assess correlates and consequences of red shiner abundance at sites where they are known to occur. Sites included in this study were distributed among 11 major river basins (Burr and Page 1986; Conner and Suttkus 1986; Cross et al. 1986) in five states, spanning 12.05 decimal-degrees of latitude and 11.42 decimal-degrees of longitude. Sites ranged in size from small pasture streams 3 m wide, to shallow, sandy-bottomed rivers as wide as 200 m, and varied in substrate, canopy,

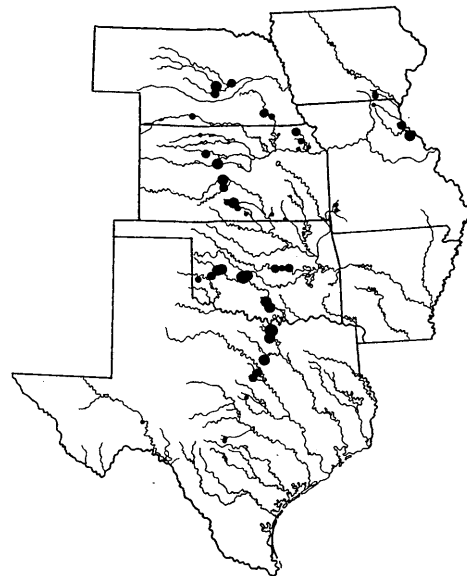


Fig. 1 Map of relative abundance of red shiners at 50 sites in the midwestern USA. Dot size reflects category of abundance. Relative abundance was divided into five equal categories over the total range of relative abundance (0.03–0.95)

depth, and current (Appendix), and overall habitat complexity (as described below).

All samples were taken by us using seines (4.8-mm mesh; up to 4.57 m long) between 2 June and 5 July 1995. At each site, all detectably distinctive microhabitats in the stream reach were intensively sampled in an effort to (1) capture as many species as possible and (2) capture species in proportion to their true abundance (Matthews 1985). Sampling at a site continued until all obvious microhabitats had been thoroughly sampled, and no additional species were captured in numerous repeated seine hauls. Sites differed in size and complexity (as defined below) and our sample effort was greater in more complex habitats as required to meet our goals. Actual collection times varied among sites from 14 min at a structurally simple 30-m reach, to 79 min at a site where 120 m of stream was sampled and habitat was complex. Length of reach sampled varied from 25 to 300 m (mode 100 m, mean 107.1 m). Number of species captured at a site was not related to reach sampled by linear regression ($P > 0.05$), but was related to time spent collecting ($P < 0.002$) as expected from our sampling protocol. Number of species captured was also not related to total individuals captured at a site (with or without red shiners included in the analysis), suggesting that although our effort varied according to site characteristics, effort at a given site allowed us to detect most species present at that site at the time of our collections.

Because we were interested in the effects of red shiners on the other species in the assemblage, assays of assemblage structure were based on the assemblage excluding red shiners, hereafter called the residual assemblage. For each residual assemblage, we assayed the following measures of assemblage structure: species richness, Shannon-Wiener diversity index, evenness, and complexity (all defined below). We also examined effects of red shiner abundance on other omnivorous minnows in the assemblage.

We have confidence that our intensive sampling protocol was more than sufficient to assay relative abundance patterns of red shiners because Angermeier and Smogor (1995) demonstrated that relatively small sampling effort is required to accurately reflect relative abundance of common species in stream fish assemblages, and that necessary effort varies little among streams. Determination of species richness in fish assemblages, however, requires considerably more effort (Angermeier and Smogor 1995). Although our sampling protocol was designed to continue collecting

until no new species were captured, we cannot dismiss the possibility that we missed some extremely rare species. We therefore used two measures of species richness of residual assemblages: actual number of species captured at a site (S), and an estimate of species richness based on rarefaction of all samples to the sample with the fewest individuals (Gotelli and Graves 1996). Rarefied estimates of species richness were calculated using EcoSim (Gotelli and Entsminger 1997), with 1,000 sampling iterations. Average species richness of 1,000 rarefied samples was used as the measure of rarefied species richness (S_{RARE}) at a site.

Diversity (H') and evenness ($E = \ln H'/S$) of the residual assemblages were calculated using PC-ORD (McCune and Mefford 1997).

Complexity of residual assemblages was quantified as the slope of the regression line of (log) relative abundance on rank abundance of species in the residual assemblage (Tokeshi 1993). This measure (hereafter called SLOPE) not only summarizes the abundance patterns within an assemblage, but has been used as a measure of assemblage structure in place of more traditional measures such as species richness or diversity (Tokeshi 1993; Sale 1996). In calculating the abundance profile, species with tied abundance in a sample were assigned the same average rank score equal to the sum of rank scores for all species in the tie divided by the number of species in the tie.

To examine the effects of red shiner abundance on other omnivorous minnows, we separated minnows in the residual assemblage into two groups: (1) insectivorous-omnivorous water column minnows (most in the genera *Cyprinella*, *Lythrurus*, and *Notropis*) and (2) herbivorous-omnivorous benthic minnows (most in the genera *Dionda*, *Pimephales*, *Hybognathus*, *Phenacobius*, and *Phoxinus*). Largely herbivorous (*Campostoma*) or macrocarnivorous (*Semotilus*) (Grossman et al. 1982) minnows were not included in either group. Separation of minnows in the residual assemblage into these groups allowed us to examine potential effects of red shiner abundance on the abundance of ecologically similar and potentially redundant (Walker 1992; Lawton and Brown 1993) species (water column minnows) as distinct from bottom-dwelling species that feed primarily on attached algae or biofilms (benthic minnows). Designation of these species was based on diet and habitat descriptions in Carlander (1969), Miller and Robison (1973), Pfeleger (1975), Grossman et al. (1982), Robison and Buchanan (1988), and on our own extensive observations in the field.

Characteristics of the stream, adjacent riparian zone, and nearby landscape were recorded at the time of collection at each site (Appendix). Historical air temperature and rainfall patterns of the county in which the site is located were compiled from United States Department of Agriculture (1941).

Using the environmental data collected in the field, we compiled an index of habitat complexity using the following categorical environmental variables (as defined in the Appendix): AMTSTR, ALGAE, MACROPHY, SAND, MUD, GRAV, RUB, BEDRK, R/PVSCH, BW. In addition we transformed the continuous variables MAXDEP and MAXWID to categorical variables. Four depth categories (DEPCAT) were established: DEPCAT 1=MAXDEP 0–50 cm; DEPCAT 2=MAXDEP 51–100 cm; DEPCAT 3=MAXDEP 101–150 cm; DEPCAT 4=MAXDEP 151–200 cm. Six width categories (WIDCAT) were established: WIDCAT 1=MAXWID 0–5 m; WIDCAT 2=MAXWID 6–10 m; WIDCAT 3=MAXWID 11–15 m; WIDCAT 4=MAXWID 20–30 m; WIDCAT 5=40–50 m; WIDCAT 6=MAXWID 100 m (discontinuities reflect actual ranges of stream widths sampled). Habitat complexity was calculated as the sum of categorical scores for the 12 variables described above. Habitat complexity thus calculated ranged from 7 to 17 for the 50 sites sampled in this study.

To examine environmental factors correlated with spatial variation in both the relative abundance of red shiners and residual assemblage structure, we performed a principal components analysis (PCA) based on a correlation matrix of habitat characteristics (described in the Appendix) by site. Site scores on PCA axes were used as independent variables in multiple linear-regression analyses (SPSS 1996) to relate site characteristics to red shiner relative abundance and residual assemblage structure. PCA was performed

using PC-ORD (McCune and Mefford 1997). Red shiner relative abundance and residual assemblage structure were also examined as a function of our index of habitat complexity using least-squares regression (SPSS 1996).

Analyses using relative abundance data were also performed with data arcsin-transformed (Krebs 1989). Because all results were nearly identical using untransformed and transformed data, untransformed data are presented for clarity.

Results

Spatial variation in red shiner relative abundance

C. lutrensis occurred in high relative abundance at sites throughout the region sampled except in central and west Texas and at the margin of the Ozark Plateau in eastern Kansas and western Missouri (Fig. 1). These sites represent local range margins for red shiners, adjacent to uplifted areas of clear, gravel bottom streams (Matthews 1980) where red shiners do not occur.

C. lutrensis ranked first in abundance at 25 of the 50 sites where the species was found, with rank abundance ranging to as low as 11th at one site (Fig. 2A). At 45 of the 50 sites, the rank of red shiners was 1–3.

The relative abundance of *C. lutrensis* in a given assemblage ranged from 0.03 to 0.95 among the 50 sites sampled. Red shiners accounted for at least 30% of indi-

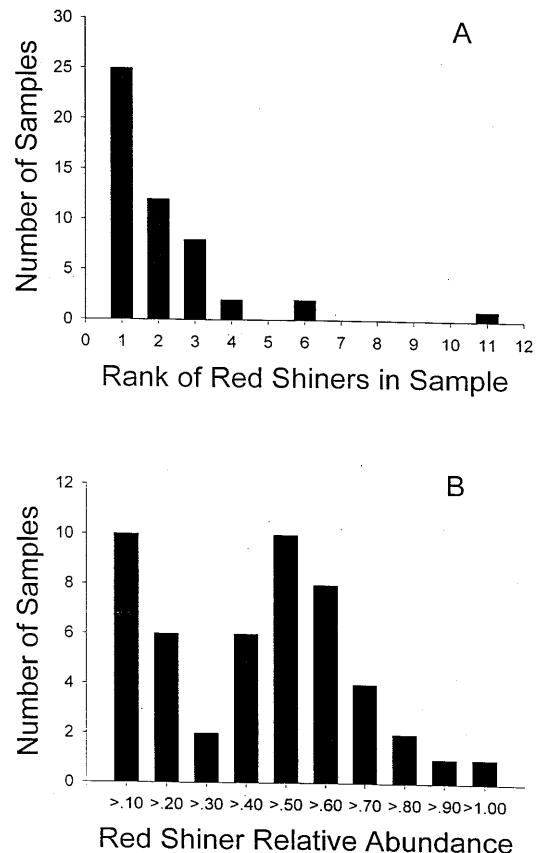


Fig. 2 Rank (A) and relative abundance (B) of red shiners at 50 sites in the midwestern USA

Table 1 Principal components analysis (PCA) based on a correlation matrix of environmental factors listed in the Appendix. Eigenvalues, variance explained, and loadings of original variables are given for six PCA axes significant by broken-stick eigenvalue (McCune and Mefford 1997)

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Eigenvalue	4.970	3.494	3.061	2.530	2.206	2.013
Percent variance explained	15.060	10.589	9.275	7.667	6.686	6.101
Loadings of original variables						
JANTEMP	-0.554	-0.158	0.022	0.073	0.327	0.309
JULYTEMP	-0.473	-0.101	0.013	0.176	0.382	0.299
RAINFALL	-0.467	0.106	-0.201	-0.095	-0.126	-0.019
REACH	0.215	-0.056	0.111	-0.277	-0.351	0.058
R/PVSCH	0.679	-0.168	-0.249	0.153	-0.064	0.362
BW	-0.144	-0.171	0.623	-0.370	-0.051	-0.189
MAXWID	0.227	-0.415	0.503	0.106	-0.420	0.291
MAXDEP	0.267	-0.034	0.677	-0.105	-0.051	0.207
WTEMP	-0.120	-0.161	-0.082	0.082	0.155	0.473
TURBID	0.334	0.248	0.167	-0.044	0.513	0.180
MAXCUR	-0.343	0.455	0.467	-0.210	-0.116	-0.107
ESTCUR	-0.039	0.277	0.699	-0.240	-0.072	-0.074
SAND	0.563	-0.222	-0.267	0.122	-0.373	-0.199
MUD	0.538	0.190	0.179	-0.256	0.511	0.112
GRAV	-0.438	0.011	0.296	-0.060	0.181	-0.332
RUB	-0.536	-0.126	0.233	0.288	0.047	0.061
BEDRK	-0.617	0.131	0.011	-0.059	0.014	0.167
BANKSTAB	-0.611	-0.164	0.178	-0.035	-0.006	0.193
ALGAE	-0.500	-0.044	-0.337	0.109	-0.093	-0.155
MACROPHY	-0.130	-0.479	0.235	-0.230	-0.044	0.018
SHADE	-0.424	0.524	-0.236	0.060	0.035	0.156
CANOPY	-0.447	0.558	-0.380	-0.282	-0.230	0.205
STROCK	-0.661	0.089	0.047	0.227	0.275	-0.179
STWOOD	0.446	0.019	-0.151	-0.585	0.033	-0.014
STCULT	0.180	0.399	0.343	0.046	0.223	0.033
AMTSTR	0.348	0.539	-0.019	-0.332	0.077	0.278
BARESOIL	0.441	0.020	-0.107	0.350	0.188	0.009
HERB	-0.178	-0.655	0.180	-0.072	0.203	0.032
SMTREE	0.014	0.362	-0.115	-0.519	0.063	-0.423
LGTREE	-0.025	0.602	-0.015	-0.031	-0.397	0.295
NATLU	-0.151	0.056	0.082	-0.144	-0.674	0.356
AGLU	0.110	-0.250	-0.402	-0.678	0.076	-0.247
URLU	0.277	0.511	0.150	0.488	0.196	0.130

viduals captured at most sites and for more than half of all individuals captured at 14 of the 50 sites (Fig. 2B).

Environmental correlates of red shiner relative abundance

PCA of site characteristics yielded six significant axes (broken-stick eigenvalue; McCune and Mefford 1997) that together explained approximately 60% of the variation in environmental characteristics measured at the sampled sites (Table 1). Least-squares multiple regression (SPSS 1996) of red shiner relative abundance at a site on site scores along the six significant PCA axes was non-significant. Thus, no suite of measured environmental factors provided a "simple" explanation for red shiner abundance throughout the region. In addition, red shiner relative abundance was not a function of habitat complexity.

Variation in residual assemblage structure as a function of red shiner relative abundance

The number of species (excluding red shiner) collected at a site ranged from 3 to 29 (mean=10.46, SD=4.66) for

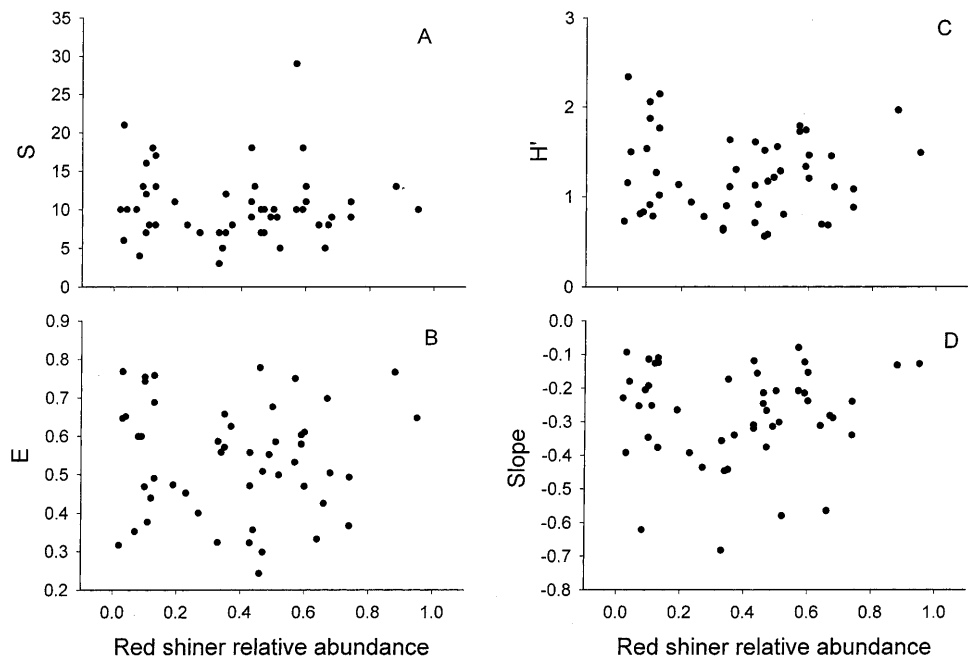
the 50 sites sampled (Fig. 3A). Average rarefied species richness of the residual assemblage ranged from 2.58 to 11.41 (mean=5.54, SD=1.99). Number of species captured and average rarefied richness were highly and significantly correlated ($r=0.798$, $P<0.001$). Neither actual number of species captured in the residual assemblage nor average rarefied richness of the residual varied significantly as a function of the relative abundance of red shiners in the entire assemblage (Fig. 3A).

Evenness of species abundances (E) in residual assemblages ranged from 0.243 to 0.778 (mean=0.538, SD=0.144). Variation in evenness was not a function of red shiner relative abundance in the entire assemblage (Fig. 3B).

Diversity (H') of residual assemblages varied from 0.560 to 2.339 (mean=1.229, SD=0.450) but that variation was not a function of red shiner relative abundance in the entire assemblage (Fig. 3C).

The slope of the log abundance versus rank curve (i.e., complexity) of residual assemblages varied from -0.683 (least complex) to -0.079 (most complex) with a mean of -0.277(± 0.140). Complexity measured in this way was not a function of relative abundance of red shiners in the entire assemblage (Fig. 3D).

Fig. 3 Structure of the residual assemblage as a function of red shiner relative abundance in the entire assemblage. Measurement of residual assemblage structure used: species richness (*S*) (A), evenness of species abundances (*E*) (B), species diversity (*H'*) (C), complexity (*Slope*) (D). See text for explanation of terms



Relative abundance of water column minnows in residual assemblages varied from 0 to 0.967 (mean=0.478, SD=0.306). Relative abundance of the residual assemblage by water column minnows was not a function of red shiner relative abundance in the entire assemblage (Fig. 4A). Relative abundance of benthic minnows in the residual assemblage varied from 0 to 0.875 (mean=0.250, SD=0.216). In contrast to the result for water column minnows, relative abundance of benthic minnows in the residual assemblage was significantly ($P<0.05$) related to relative abundance of red shiners (Fig. 4B) such that assemblages more dominated by red shiners had relatively larger numbers of benthic minnows in the residual assemblage. Variation in red shiner relative abundance explained 9.8% of the variation in benthic minnow relative abundance.

Relationship of residual assemblage structure to environmental characteristics

Suites of environmental characteristics summarized on PCA axes explained from 9.3 to 11.8% of the variation in three measures of residual assemblage structure. In each case, however, the relationship between environment and residual assemblage structure involved different PCA axes. Average rarefied species richness (*S* RARE) of residual assemblages was significantly related to PCA axis 1 (Fig. 5) which was correlated ($r>0.5$) primarily with January temperature, stream morphology, substrate, algae, and bank stability (Table 1, Fig. 5). *S* RARE tended to be greater at sites with higher winter temperatures, riffle pool morphology, higher bank stability, and rubble and or bedrock substrate with instream rock structure.

Variation in evenness in abundance of the residual assemblage (*E*) was significantly related to environmental

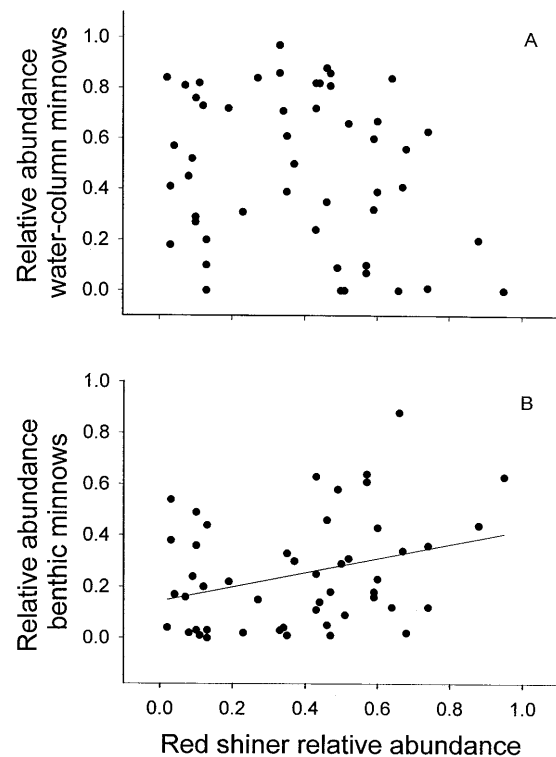


Fig. 4 Relative abundance of water column (A) and benthic (B) minnows in the residual assemblage as a function of relative abundance of red shiners in the entire assemblage. Least-squares regression of benthic minnow abundance on red shiner abundance significant at $P<0.05$ ($R^2=0.098$)

Table 2 Residual assemblage structure as a function of environmental characteristics summarized by PCA axes and as a function of habitat complexity. Values are R^2 values significant at $P < 0.05$ by multiple linear regression (NS not significant)

Residual assemblage structure	PCA						Habitat complexity
	1	2	3	4	5	6	
S	NS	NS	NS	NS	NS	NS	0.093
S RARE	0.093	NS	NS	NS	NS	NS	NS
E	NS	0.098	NS	NS	NS	NS	NS
H'	NS	NS	NS	NS	NS	NS	NS
Slope	NS	NS	NS	NS	NS	NS	0.102
Water column minnows	NS	NS	NS	NS	0.118	NS	NS
Benthic minnows	NS	NS	NS	NS	NS	NS	NS

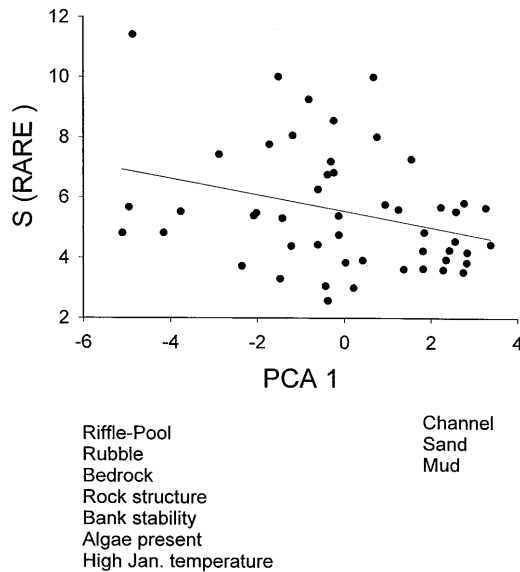


Fig. 5 Relationship of average rarefied species richness S (RARE) in the residual assemblage to environmental PCA axis 1. See text for explanation of S (RARE) and the Appendix for a description of environmental characteristics

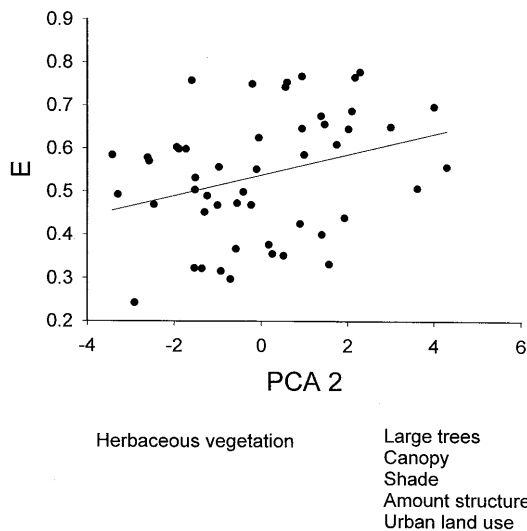


Fig. 6 Relationship of evenness (E) in the residual assemblage to environmental PCA axis 2. See text for explanation of E and the Appendix for description of environmental characteristics

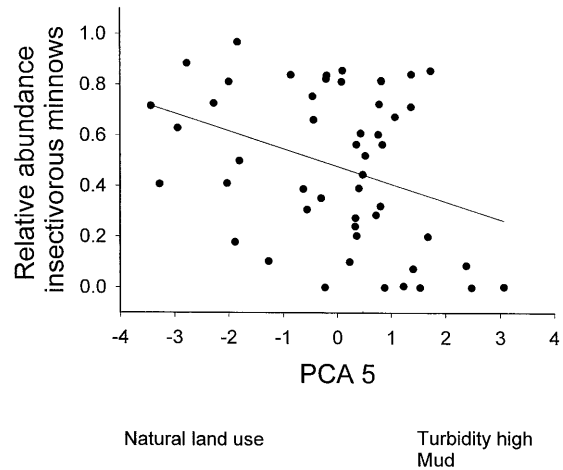


Fig. 7 Relationship of relative abundance of water column minnows in the residual assemblage to environmental PCA axis 5. See the Appendix for description of environmental characteristics

characteristics that loaded on PCA axis 2 (Table 2, Fig. 6). These characteristics were primarily related to the riparian zone and to total amount of instream structure. Evenness of the residual assemblage tended to be higher at sites with large trees, higher canopy cover and shade, and greater amounts of instream structure of all types (Table 1, Fig. 6).

Relative abundance of water column minnows in residual assemblages was significantly related to environmental characteristics loading on PCA axis 5 (Table 2, Fig. 7). These included: turbidity, mud substrate, and natural land use of the surrounding riparian zone (Table 1). Relative abundance of water column minnows in residual assemblages was lower at turbid sites with mud substrate and higher at sites with natural land use (Table 1, Fig. 7).

Residual assemblage structure was also explained in part by habitat complexity (Table 2). Both species richness (S) and complexity of the residual assemblage (SLOPE) were greater in more complex habitats (Fig. 8), with variation in habitat complexity accounting for 9–10% of variation in residual assemblage structure.

Discussion

Red shiners have historically been highly abundant in low-gradient streams of midwestern North America

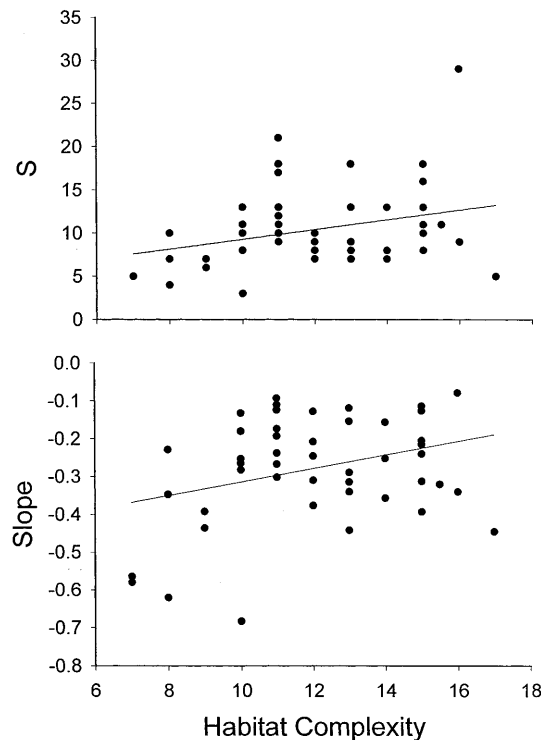


Fig. 8 Relationship of species richness (S) (A) and complexity (Slope) (B) to habitat complexity. See text for explanation of terms

where they are native (Laser and Carlander 1971; Smith 1979; Matthews 1980; Mayden 1989; Pigg et al. 1997), and at sites where they have been introduced (Page and Smith 1970; Smith 1979; Jennings and Saiki 1990; Gido et al. 1997). Among the sites sampled in this study, all within the native range, *C. lutrensis* was the most abundant species at half of the sites, and numerically dominated (accounted for >50% of all individuals captured) 28% of the assemblages.

The relative abundance of red shiners showed no overall geographic pattern, except an apparent local range-margin effect in central and west Texas and in Ozark-margin streams where red shiners were less likely to dominate assemblages than in other parts of the range. This unpredictable geographic pattern of red shiner dominance suggests that local rather than biogeographic factors control local abundance of red shiners.

Despite the suggestion of local control of dominance, relative abundance of red shiners in an assemblage was not predictable from the environmental factors measured in this study or from our measure of habitat complexity. This is consistent with observations in other studies that *C. lutrensis* is tolerant of a wide range of conditions and occurs across a wide variety of microhabitats (Matthews and Hill 1979, 1980; Matthews 1985). Although Brown et al. (1995) suggested that spatial variation in abundance of many species may be attributable to variation in a few “niche axes,” no such niche axes were easily defined by our data. There may be several reasons for this lack of correlation. First, we may not have measured

some relevant environmental factors, although these same factors were informative in explaining a proportion of overall assemblage composition and emergent structure in the entire set of 65 midwest fish assemblages (Marsh-Matthews and Matthews 2000), as well as some measures of residual assemblage structure in this study. More likely, the lack of explanation of red shiner abundance patterns by environmental factors reflects the wide range of conditions tolerated by *C. lutrensis* (Matthews 1985, 1987; Cross and Collins 1995). *C. lutrensis* clearly represents what Brown (1995) called a “jack-of-all-trades... [and] master of all”.

Spatial variation in relative abundance of red shiners observed in this study may reflect underlying spatial variation in some complex suite of environmental characters, environmental extremes, predictability, or even background temporal variation in population size. Ives and Klopfer (1997) have demonstrated that apparent patterns of spatial variation in abundance may, in fact, result from stochastic temporal variation in populations that show weak density dependence. Although our study was designed to preclude seasonal differences among collections (all were taken in early summer), we have no data on background stochastic variation in sizes of local populations within these assemblages. Other Midwest fish assemblages, however, do exhibit short-term temporal variation in assemblage composition and relative abundance of species of the order of a 30–50% change between monthly samples (Taylor et al. 1996; E. Marsh-Matthews and W.J. Matthews, unpublished data).

Only one component of residual fish assemblage structure (relative abundance of benthic minnows) was found to correlate with dominance of red shiners in an assemblage. This lack of apparent influence by red shiners on most measures of assemblage structure of other fishes is somewhat surprising because Cross and Collins (1995, p. 57) noted that, within its native range, *C. lutrensis* is “most numerous where few other kinds of fish occur”. We found, however, that relative abundance of red shiners was not correlated with species richness (either assayed by direct capture or calculated by rarefaction), evenness, diversity, or complexity of the residual assemblage. This lack of correlation suggests that *C. lutrensis* has little role in structuring assemblages of other fishes within its native range. Evans (1989) found a similar lack of apparent effect of a numerically dominant grasshopper species.

The apparently minimal effect of *C. lutrensis* in native communities is in sharp contrast to its effects on assemblages at sites where it has been introduced. At those sites, changes in assemblage structure (primarily loss of native species) have been attributed to competition with (Greger and Deacon 1988) or predation on larvae by (Ruppert et al. 1993) red shiners, as well as to hybridization between red shiners and closely related species (Burr and Page 1986; Larimore and Bayley 1996).

Differential effects of red shiner dominance in native versus introduced situations raises the question of the role of *C. lutrensis* in native assemblages. The lack of

apparent influence on assemblage structure despite their overall numerical dominance suggests that within natural assemblages, competitive and predatory interactions between *C. lutrensis* and other assemblage elements are moderated by local conditions or by coevolved habitat partitioning or behaviors. Although Brown (1995) has cautioned that ecologists have overestimated the degree to which natural assemblages are coevolved, our results imply that natural communities differ from artificial assemblages in the degree to which a single, dominant species can influence assemblage structure. The degree of temporal variation in composition of local midwest fish assemblages (Matthews and Hill 1980; Taylor et al. 1996) suggests that such assemblages may be more loosely coevolved than stream assemblages in Ozark uplands (Gorman 1992). Nonetheless, the common elements of those assemblages may have been sufficiently predictable in presence (if not in abundance) over time that local biotic interactions have resulted in coevolved habitat partitioning or behaviors that prevent red shiners from controlling assemblage structure despite their numerical dominance. The drainage patterns of the Great Plains have been in present locations since at least the Pleistocene with little evidence of stream captures (Cross et al. 1986); thus, local native species have a substantial history of cooccurrence.

The one significant effect of red shiner abundance detected in this study was an increase in relative number of benthic minnows in the residual assemblage with higher relative abundance of red shiners in the entire assemblage. This result does not simply reflect an inverse relationship between benthic and water column minnows in the residual assemblage because relative abundance of water column minnows was not related to red shiner relative abundance. The positive relationship between red shiners and benthic, largely herbivorous minnows could have several causes. Environmental characteristics conducive to high red shiner abundance could also favor benthic minnows. Given that neither red shiner nor benthic minnow abundance was found to vary as a function of environmental conditions measured in this study, we cannot support this explanation with our data. Alternatively, red shiners may in some way enhance benthic minnow densities (or vice versa) via indirect biotic effects. Gido and Matthews (in press) suggest that red shiners affect productivity in artificial stream systems. At this time, however, the relationship between red shiner and benthic minnow abundances remains unexplained.

Within its native range, *C. lutrensis* dominates assemblages but does not appear to control assemblage structure. Although assemblages dominated by red shiners tended to have a greater abundance of benthic minnows, they otherwise did not have fundamentally different structure than those in which red shiners were in low numbers. In fact, residual assemblage characteristics were more readily explained by environmental characteristics and habitat complexity than by red shiner abundance. However, it is clear that *C. lutrensis* is a species

that may be “benign” within its native range, but can severely impact assemblages where it is introduced, and provides yet another example of the need for caution in the introduction of exotics.

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Appendix Characteristics of local riparian zone and stream reach recorded for each site

JANTEMP	Mean annual January temperature for the county in which the site is located [taken from United States Department of Agriculture (1941)]
JULYTEMP	Mean annual July temperature for the county in which the site is located [taken from United States Department of Agriculture (1941)]
RAINFALL	Mean annual rainfall for the county in which the site is located [taken from United States Department of Agriculture (1941)]
REACH R/PVSCH	Length of stream reach sampled Designation of primary morphology of stream reach sampled as either riffle pool or channel structure
BW	Presence of backwaters
MAXWID	Maximum width of stream at the site sampled
MAXDEP	Maximum depth of stream at the site sampled
WTEMP	Water temperature measured at the time site sampled
TURBID	Turbidity; categorized as low, moderate, or high
MAXCUR	Current speed (m/s) at the point in sample reach with the fastest current
ESTCUR	Relative overall current in the sample reach; categorized as none, slow, moderate, or swift
SAND	Presence or absence of sand substrate
MUD	Presence or absence of mud substrate
GRAV	Presence or absence of gravel substrate
RUB	Presence or absence of rubble substrate
BEDRK	Presence or absence of bedrock substrate
BANKSTAB	Bank stability; categorized as low or high
ALGAE	Presence or absence of attached algae or floating mats
MACROPHY	Presence or absence of macrophytes
SHADE	Categorized as none, partial, or near complete
CANOPY	Percent canopy cover estimated at time of collection
STROCK	Presence of large rock structure in stream
STWOOD	Presence of large woody debris in stream
STCULT	Presence of discarded man-made debris in stream
AMTSTR	Relative amount of all types of structure combined; categorized as none, minimal, moderate, or extensive
BARESOIL	Presence or absence of bare soil on stream bank
HERB	Presence or absence of herbaceous vegetation on stream bank
SMTREE	Presence or absence of small trees (ca 3 m or less in height) on stream bank

LGTREE	Presence of absence of large trees (more than 3 m in height) on stream bank.
NATLU	Natural land use; recorded as present if a large portion of riparian zone appeared undisturbed by agricultural use or urban development
AGLU	Agricultural land use; recorded as present if landscape surrounding riparian zone in use for grazing or row crops
URLU	Urban land use; recorded as present if landscape surrounding riparian zone developed for housing or commerce

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